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Genetic detection of node of first fruiting branch in crosses of a cultivar with two exotic accessions of upland cotton

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Abstract Flowering time has biological and agricultural significance for crops. In Upland cotton (*Gossypium hirsutum* L.), photoperiodic sensitivity is a major obstacle in the utilization of primitive accessions in breeding programs. Quantitative trait loci (QTLs) analysis was conducted in two F_2 populations from the crosses between a day-neutral cultivar Deltapine 61 (DPL61) and two photoperiod sensitive *G. hirsutum* accessions (T1107 and T1354). Node of first fruiting branch (NFB) was used to measure relative time of flowering. Different flowering time genetic patterns were observed in the two populations. Two QTLs were found across five scoring dates, accounting 28.5 (*qNFB-c21-1*) and 15.9% (*qNFB-c25-1*) of the phenotypic variation at the last scoring date in Pop. 1107 (DPL61 by T1107); whereas, one major QTL (*qNFB-c25-1*) can be detected across five scoring dates, explained 63.5% of the phenotypic variation at the last scoring date in Pop. 1354 (DPL61 by T1354). QTLs with minor effects appeared at various scoring date(s), indicating their roles in regulating flowering at a lower or higher node number. Genetic segregation analysis and QTL mapping results provide further information on the mechanisms of cotton photoperiodic sensitivity.

Keywords Cotton · Germplasm · Flowering time · QTL

Abbreviations

DPL61	Deltapine 61
LOD	Logarithm of odds
NFB	Node of first fruiting branch
T1107	Texas accession 1107
T1354	Texas accession 1354

Introduction

Cotton (*Gossypium* spp.) is the leading natural fiber crop of the world. A decline in genetic diversity of Upland cotton (*G. hirsutum* L.) cultivars and the need to broaden the genetic base of cotton germplasm useful for the improvement of lint yield, fiber quality, and biotic or abiotic stresses has been reported as an area of concern by a number of cotton researchers (Van Esbroeck et al. 1999; Bowman 2000; Iqbal et al. 2001; Gutiérrez et al. 2002). Incorporating favorable alleles, genes or gene complexes from wild relatives

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or accessions has been a high strategic priority for practical crops improvement (Feuillet et al. 2008). However, like other crops, photoperiodic sensitivity is a major obstacle in the utilization of primitive germplasm in cotton (Stephens et al. 1967; Holley and Goodman 1988; McCarty and Jenkins 1992; Uga et al. 2007).

Plant flowering time is an adaptive trait with biological and agricultural significance (Murfet 1977). Conventional genetic analysis on cotton photoperiodic sensitivity has been conducted in different intraspecific (*G. hirsutum*) hybrids. Flowering time has been found under multigenic control, segregation patterns were different among populations (Lewis and Richmond 1957; Waddle et al. 1961; Kohel and Richmond 1962; Kohel et al. 1965). In practice, developing flowering types from primitive photoperiodic accessions has been carried out by backcrossing and selection procedures (McCarty et al. 1979; McCarty and Jenkins 1992). However, the numbers of loci controlling genetic variation and their genetic map positions have not been well characterized. With the advent of molecular marker technology and molecular linkage maps in cotton (Reinisch et al. 1994; Mei et al. 2004; Rong et al. 2004, 2007; Guo et al. 2007), molecular genetic studies on photoperiodic sensitivity by quantitative trait loci (QTLs) mapping are possible. Molecular mapping flowering time using populations with different segregating pattern will not only enhance the understanding of the diverse mechanisms of photoperiodic sensitivity but also hold the possibility of finding the common locus/loci in different populations, which will facilitate understanding the domestication of the trait and aid in marker assistant selections of day-neutral lines.

In cotton, main stem node of first fruiting branch (NFB) was positively related to flowering time and used as a practical measurement of earliness. By comparing with different measurements of earliness in cotton, Ray and Richmond (1966) concluded that NFB was the most reliable and practical measurement. Considering the heritability and correlation with final picking, Low et al. (1969) also suggested using NFB as a criterion to measure earliness.

Our previous genetic analysis of cotton photoperiodic sensitivity in one photoperiodic primitive stock (T701) by mapping QTLs related to NFB (Guo et al. 2008a) indicated that flowering time was a complex trait and controlled by multiple genes, as reported in other plants (Yano et al. 2001; Komeda 2004). In this research, two more populations, generated from the crosses between the common day-neutral commercial cultivar Deltapine 61 (DPL61) and two photoperiod sensitive accessions (T1107 and T1354), with different photoperiodic response, were further characterized by measuring NFB at five dates ranging from 73 to 129 days after planting (DAP). QTLs related to NFB were detected and compared across different populations. Genetic segregation analysis and QTL mapping results provide further information on the mechanisms of cotton photoperiodic sensitivity.

Materials and methods

Experimental populations and phenotypic data collection

Two intraspecific (*G. hirsutum*) F_2 populations were developed by crossing DPL61 (PI 607174) as female parent with T1107 (PI 529941) and T1354 (PI 530082) and selfing the F_1 plants in the winter nursery at Tecoman, Mexico. T1107 was collected in Mexico, while T1354 was collected in Puerto Rico (USDA-ARS Germplasm Resources Information Network, http://www.ars-grin.gov). Both accessions flower in their original collection locations but do not flower under the normal long days of summer in Mississippi. F_2 populations were planted in the field on May 16, 2006 at the Plant Science Research Center, Mississippi State, MS (33.4 N, 88.8 W). Standard cultural, insect and weed control practices were followed. Plants in each population were tagged individually at the end of July and the main stem NFB was determined at the following five dates: July 28 (73 DAP), August 8 (84 DAP), August 25 (101 DAP), September 5 (112 DAP), and September 22 (129 DAP). We scored 125 plants in the cross DPL61 × T1107 designated as population 1107 (Pop. 1107) and 101 plants in the cross DPL61 × T1354 designated as population 1354 (Pop. 1354). At each scoring date, F_2 plants that did not flower were given a score of one node higher than the then highest NFB for QTL analysis. Similar phenotypic value assignment was widely used in QTL analyses of flowering time in rice (Gu and Foley 2007) and *Brassica* (Long et al. 2007; Okazaki et al. 2007), and seed germination in sunflower (Wills and Burke 2007).

In order to detect NFB of F_1 and photoperiod sensitive parental plants, which would not generate flowers in field plots due to low temperature after normal harvest time, three parental lines and two F_1 crosses were planted in a greenhouse at Mississippi State (MS) under the natural day length environment on August 13, 2006. The greenhouse plants were grown in pots (20 cm diameter by 30 cm depth) and arranged as a completely randomized design. Each genotype was regarded as a treatment and individual plant as replicate (3–17). NFB were scored on December 15, 2006. Day length decreased from 13 h 9 min to 9 h 57 min during this time.

DNA markers and laboratory assay

Leaves were collected from individual F_2 plants and bulks of parents and F_1s. Genomic DNA was isolated from frozen dried leaf samples using DNeasy Mini Kit (Qiagen Inc., Valencia, CA, USA) following the manufacture protocol. A total of 1,165 fluorescent-labeled SSR primers were used for parental polymorphism screening. These SSR primers included BNL, JESPR, MGHES, TMB, CIR, and NAU series (Blenda et al. 2006; http://www.cottonmarker.org/). PCR reaction, amplification, and capillary electrophoresis analysis with an ABI 3100 genetic analyzer (Applied Biosystems, Foster City, CA, USA) followed the protocol of Gutiérrez et al. (2002). The marker acronyms were according to Nguyen et al. (2004). After the construction of a tentative linkage map by BNL markers and the estimation of putative QTL positions and effects, all other polymorphic markers (JESPR, MGHES, TMB, CIR, and NAU) on the putative QTL located chromosomes were added for genotyping each of the two populations. In total, 191 and 175 polymorphic markers were used for screening F_2 individuals in Pop. 1107 and Pop. 1354, respectively.

Linkage map construction and QTL detection

A genetic linkage map was constructed by Joinmap 4.0 (Van Ooijen 2006). A minimum LOD score ($\log_{10}$ of the likelihood odds ratio) of 5.0 was set as a threshold to allocate marker loci into linkage groups, and a maximum recombination fraction of 0.40 was employed as general linkage criteria to establish linkage groups. The Kosambi function was used to order markers and estimate map unit distances (Kosambi 1944). Segregation distortion at each marker locus was tested against the expected segregation ratios (1:2:1 for co-dominant markers and 3:1 for dominant markers) using a *chi*-square goodness of fit test. Chromosomal assignments of linkage groups were achieved by CMD (Cotton Microsatellite Database) inquiry (http://www.cottonmarker.org), deletion analysis-based chromosomal assignment of TMB series markers (Guo et al. 2008b), comparison to the published integrated molecular maps (Nguyen et al. 2004; Lacape et al. 2005; Wang et al. 2006; Guo et al. 2007), and our unpublished data. QTL analysis was conducted by MapQTL 5.0 (Van Ooijen 1999, 2004) with interval mapping. Statistically significant associations between markers and trait (NFB) were detected by Kurskal–Wallis (K–W) analysis-based non-parametric genome scan. A significant QTL was defined with the LR (Log likelihood ratio) threshold larger or equal to 13.8 (equal to LOD score 3.0), which restricted the occurrence of a type I statistical error to <5% (Jiang et al. 1998). A suggestive QTL was defined with LR value between 9.2 and 13.8, i.e., $2.0 \leq \text{LOD value} < 3.0$ according to the guidelines for interpreting and reporting linkage results (Lander and Kruglyak 1995). Confidence intervals (90–95%) associated with QTL locations were set as the map interval, corresponding to one LOD decline on either side of the peak. A mixed linear model-based QTLNetwork 2.0 program (Yang and Zhu 2005) was used to determine epistatic QTLs with a permutation test of 1,000 times at a significance level of $P = 0.005$. QTL graphs were drawn by MapChart 2.2 (Voorrips 2002). The typical QTL nomenclature suggested by McCouch et al. (1997) was followed, which was a designation of '*q*' followed by an abbreviation of the trait name (NFB), then the chromosome on which it was located, and the number of the detected QTL on the chromosome. Genetic effects associated with single marker and multiple markers were conducted by regression analyses and stepwise regression analyses, respectively, using 'PROC GLM' command of SAS 9.1 (SAS Institue Inc., NC, USA).

Results and discussion

Fruiting in commercial Upland cotton cultivars, like the common female parental line DPL61, follows a

well defined pattern. The first fruiting branch usually develops at main stem node seven. Thereafter, each succeeding main stem node above this fruiting branch node will normally produce a fruiting branch. Under commercial production, cultivars in Mississippi usually produce 19–22 main stem nodes, which results in 12–15 fruiting branches. In general, there are 3 days between initiation of successive main stem nodes and 6 days between successive fruiting buds on a fruiting branch. The first fruiting bud (square) is visible at about 36 DAP and the first open flower usually occurs on main stem node seven at about 66 DAP.

Flowering response

In this study, we had two F_2 populations between a day-neutral cultivar and two photoperiod sensitive accessions. Both populations segregated for NFB, an indirect measure of flowering time (Ray and Richmond 1966; Low et al. 1969). Similar to commercial cultivars, once an F_2 plant produced a fruiting node, it usually continued to produce fruiting branches at each succeeding main stem node. The appearance of NFB, unlike commercial cultivars, varies between individuals in the population. We scored each F_2 population at 73, 84, 101, 112, and 129 DAP.

Data in Table 1 indicated that as the season progressed, more and more plants in the F_2 populations developed NFB (Table 1). At the first date (73 DAP), Pop. 1107 segregated into 26.4, 6.4, 0.8, and 0% of plants with NFB at nodes 5–9, 10–12, 13–18, and 19–29, respectively, and 66.4% of the plants without a fruiting branch. At the last date (129 DAP), this population segregated into 28.0, 14.4, 20.0, and 14.4% of plants with NFB at nodes 5–9, 10–12, 13–18 and 19–29, respectively. There were 23.2% plants in the population did not initiate a discernable NFB during the season (Table 2). Pop. 1354 flowered quite differently from Pop. 1107. At the first date (73 DAP), there were 8.9, 5.9, 4.0, and 0% of the plants with NFB at nodes 5–9, 10–12, 13–18, and 19–29, respectively, 81.2% of the plants did not have any NFB. At 129 DAP, Pop. 1354 segregated into 8.9, 5.9, 6.9, and 14.9% of the plants with NFB at nodes 5–9, 10–12, 13–18, and 19–29, respectively. There were 63.4% of the plants that did not initiate a discernable NFB during the season (Table 2). Phenotypic distribution in both populations displayed an abnormal distribution. Considering the concern of declining QTL detection sensitivity by data transforming (Mutschler et al. 1996) and similar QTL mapping results by comparing transformed and non-transformed data (Shen et al. 2006), we chose to use the original data for QTL analysis in this study like previous reports (Wright et al. 1998, 1999; Guo et al. 2008a).

The dynamic trends of F_2 plants with NFB were also different in the two populations. In Pop. 1107, plants continuously produced NFB at higher main stem nodes as the season progressed from 73 to 129 DAP (Table 1). In Pop. 1354, no more plants produced NFB after August 25 (101 DAP); this number remained stable till our last recording date (Table 1).

Table 1 Distribution frequency of node of first fruiting branch (NFB) in two F_2 segregating populations

Population	NFB	Date				
		July 28 (73 DAP)	August 8 (84 DAP)	August 25 (101 DAP)	September 5 (112 DAP)	September 22 (129 DAP)
Pop. 1107	5–9	33	35	35	35	35
	10–12	8	18	18	18	18
	13–18	1	11	19	24	25
	19–29	–	1	4	8	18
	NF	83	60	49	40	29
Pop. 1354	5–9	9	9	9	9	9
	10–12	6	6	6	6	6
	13–18	4	6	7	7	7
	19–29	–	2	14	15	15
	NF	82	78	65	64	64

DAP, Days after planting; NF, Number of plants that did not initiate a fruiting branch by specific DAP

Table 2 Percentage of plants with a fruiting branch (FB) at specified nodes in two F_2 populations at 129 DAP

Node	Pop. 1107		Pop. 1354	
	% with FB	Cumulative % with FB	% with FB	Cumulative % with FB
5	0.80	0.80	0	0
6	5.60	6.40	0	0
7	10.40	16.80	1.98	1.98
8	5.60	22.40	1.98	3.96
9	5.60	28.00	4.95	8.91
10	2.40	30.40	1.98	10.89
11	7.20	37.60	2.97	13.86
12	4.80	42.40	0.99	14.85
13	1.60	44.00	1.98	16.83
14	0.80	44.80	1.98	18.81
15	3.20	48.00	0.99	19.80
16	4.80	52.80	0	19.80
17	5.60	58.40	0	19.80
18	4.00	62.40	1.98	21.78
19	3.20	65.60	0.99	22.77
20	2.40	68.00	2.97	25.74
21	1.60	69.60	2.97	28.71
22	0	69.60	2.97	31.68
23	0.80	70.40	2.97	34.65
24	0.80	71.20	0.99	35.64
25	1.60	72.80	0	35.64
29	1.60	74.40	0	35.64
27	0.80	75.20	0.99	36.63
28	0	75.20	0	36.63
29	1.60	76.80	0	36.63
No FB	23.20		63.37	

Normally, plants with NFB $\leq$ 12 can produce mature bolls and thus were categorized as day-neutral plants; whereas, plants with NFB > 12 did not produce mature bolls before harvest and were categorized as photoperiod sensitive plants. In Pop. 1107, 42.40% of the plants had NFB $\leq$ 12; whereas, only 14.85% of plants in Pop. 1354 had NFB $\leq$ 12 (Table 2). Pop. 1107 segregated into a 9:7 ratio for NFB > 12 to NFB $\leq$ 12 suggesting the interaction of two major genes controlling day neutrality. Pop. 1354 did not fit a simple genetic segregation ratio, suggesting a complex of genes involved in photoperiodic sensitivity. However, both populations finished the development of day-neutral plants (plants with NFB $\leq$ 12) before 84 DAP (August 8).

In the 2006 field growing season, the day time length decreased to 12 h 9 min at 129 DAP, thus the two F_2 segregating populations were generally grown under long days. In the greenhouse trial for parents and F_1s, the day length decreased from 13 h 9 min to 9 h 57 min which were mainly short days. DPL61 was insensitive to day time length change, plants under both field and greenhouse photoperiods had NFB around seven. The two photoperiod sensitive accessions T1107 and T1354 remained vegetative until late into the typical field growing season, and had NFB of 13.7 ± 1.97 and 17.0 ± 1.91, respectively in the greenhouse. The F_1 plants had NFB at node 9.3 ± 1.53 for DPL61 $\times$ T1107 and at node 8.6 ± 0.55 for DPL61 $\times$ T1354 in the greenhouse trial.

Linkage maps

There were 191 SSR markers used for linkage map construction in Pop. 1107. Of these, 168 markers were assigned to 35 linkage groups covering 972 cM. For Pop. 1354, a total of 175 SSR markers were used for linkage map construction. Of these, 149 markers were assigned to 30 linkage groups spanned a recombination length of 790 cM. The marker order of our linkage maps agreed with previous publications (Nguyen et al. 2004; Lacape et al. 2005; Guo et al. 2007). In cotton linkage maps were constructed by interspecies crosses (*G. hirsutum* $\times$ *G. barbadense*) derived populations (Rong et al. 2004; Guo et al. 2007). The narrow genetic base of Upland cotton (*G. hirsutum*) germplasm (Bowman 2000; Gutiérrez et al. 2002) and the limited number of available polymorphic molecular markers (An et al. 2007) were the two most critical restriction factors for the construction of the wide coverage linkage maps at the intraspecies level. Because of the none-association between available polymorphic BNL markers and NFB or the lack of coverage of polymorphic BNL markers on specific chromosomes, chromosomes 1, 5, 7, and 13 of Pop. 1107 and chromosomes 1, 3, 6, 7, 10, 13, 20, and 22 of Pop. 1354 did not anchor any linkage groups.

QTL mapping for NFB

QTLs detected in Pop. 1107 were located on chromosomes 2, 9, 10, 19, 21, 23, 25, and one unknown linkage

group (Fig. 1). All of the markers significantly ($P = 0.05$) associated with NFB from K–W analysis were located on these chromosomes. Two larger effect QTLs detected at all five scoring dates were identified on chromosomes 21 and 25. They had LOD scores of 7.9 (*qNFB-c21-1*) and 4.5 (*qNFB-c25-1*), accounted for 28.5 and 15.9% of the phenotypic variation with additive effects of −6.5 and −3.6, respectively at 129 DAP (Fig. 2).

As the total number of plants with NFB increased over time in the population, the percentage of variation explained by a particular QTL changed and the degree of additive or dominance effects also varied consequently (Fig. 2). The *qNFB-c25-1* had an increasing R^2 and LOD score while *qNFB-c21-1* had a decreasing R^2 and LOD score across the scoring dates, which probably influenced by plants in the populations with higher NFB. This was to be expected if additional QTLs for higher NFB under long days were associated with flowering at higher main stem nodes. As the season progressed and days became shorter, additional plants in the population flowered, which was probably because additional genes under QTLs responsible for higher NFB were activated by the reduced daytime length. In this research, suggestive QTLs associated with a higher NFB detected on chromosomes 2, 9, and 19 (Figs. 1, 2) might play such a role. Another suggestive QTL (*qNFB-cna-1*) with unknown chromosome location and smaller effect (<10%) was not detected after the third scoring date (101 DAP), which probably resulted from plants flowering after 101 DAP changed the whole population NFB segregation pattern, thus this QTL could not be detected at the specific LOD threshold (Figs. 1, 2). Moreover, two suggestive QTLs (*qNFB-c10-1* and *qNFB-c23-1*) were also detected at all scoring dates, but less phenotypic variation was explained (∼10%), indicating their relatively smaller effects (Figs. 1, 2).

QTLs detected in Pop. 1354 were located on chromosomes 9, 15, 21, 23, and 25 (Fig. 1). All of the markers significantly ($P = 0.05$) associated with NFB from K–W analysis were located on these chromosomes. The major QTL, *qNFB-c25-1*, was detected at all stages with an LOD score of 16.6 and accounted for 63.5% of the phenotypic variation on the last scoring date (129 DAP) (Figs. 1, 3). Similar to Pop. 1107, other QTLs were detected with relatively smaller effects and explained less of the total phenotypic variation (Figs. 1, 3). Two of them were only detected at 73 DAP (*qNFB-c9-1* and *qNFB-c23-1*) (Fig. 1), and two others were detected from 101 to 129 DAP (*qNFB-c15-1* and *qNFB-c21-1*). The later two seemed to be associated with NFB at higher node number.

As the season progressed, the day length was becoming shorter. For photoperiod sensitive plants, the initiation of NFB was triggered when the photoperiod is suitable. Since some plants produced the first fruiting branch at lower nodes and some plants produced the first fruiting branch at higher nodes, we could assume that the mechanisms triggering production of fruiting branches was activated in individual plants at a different time (lower vs. higher nodes) mainly due to the constantly changing day time length. Thus, plants in the F_2 populations expressed different QTL alleles related to NFB. The major effective QTLs across all dates should be associated with lower NFB, but as QTLs regulate flowering at higher nodes were able to be discerned in the population as days progressed, the R^2 of the major QTLs might change, which were reflected in Figs. 1–3 in both populations. Lewis and Richmond (1957) discovered that even after the proper photoperiod for flowering had been provided, there were still differences of flowering time between photoperiod sensitive accessions and day-neutral lines. This phenomenon was hypothesized to be controlled by lateness factors not associated with day length. In the greenhouse study, we found that the photoperiod sensitive parents flowered around NFB 14 and 17 in accession 1107 and 1354, respectively. Therefore, there were flowering time differences between these two accessions, which appeared to be late and very late, respectively, in initiating a fruiting branch under essentially short day conditions, indicating the presence of possible lateness factors. However, the major QTLs detected in this study might be responsible for the plants' response to photoperiod, rather than for lateness factors. Advanced experiments under short day growing conditions would be helpful to further verify the functions of these QTLs.

The common QTL (*qNFB-c25-1*) in both populations shared the same marker JESPR224-191 in their intervals and marker BNL0150-122 on the corresponding linkage map. Another QTL (*qNFB-c21-1*) detected across all five scoring dates in Pop. 1107 also had a corresponding one in Pop. 1354, but it was only detected after 101 DAP. The same marker intervals

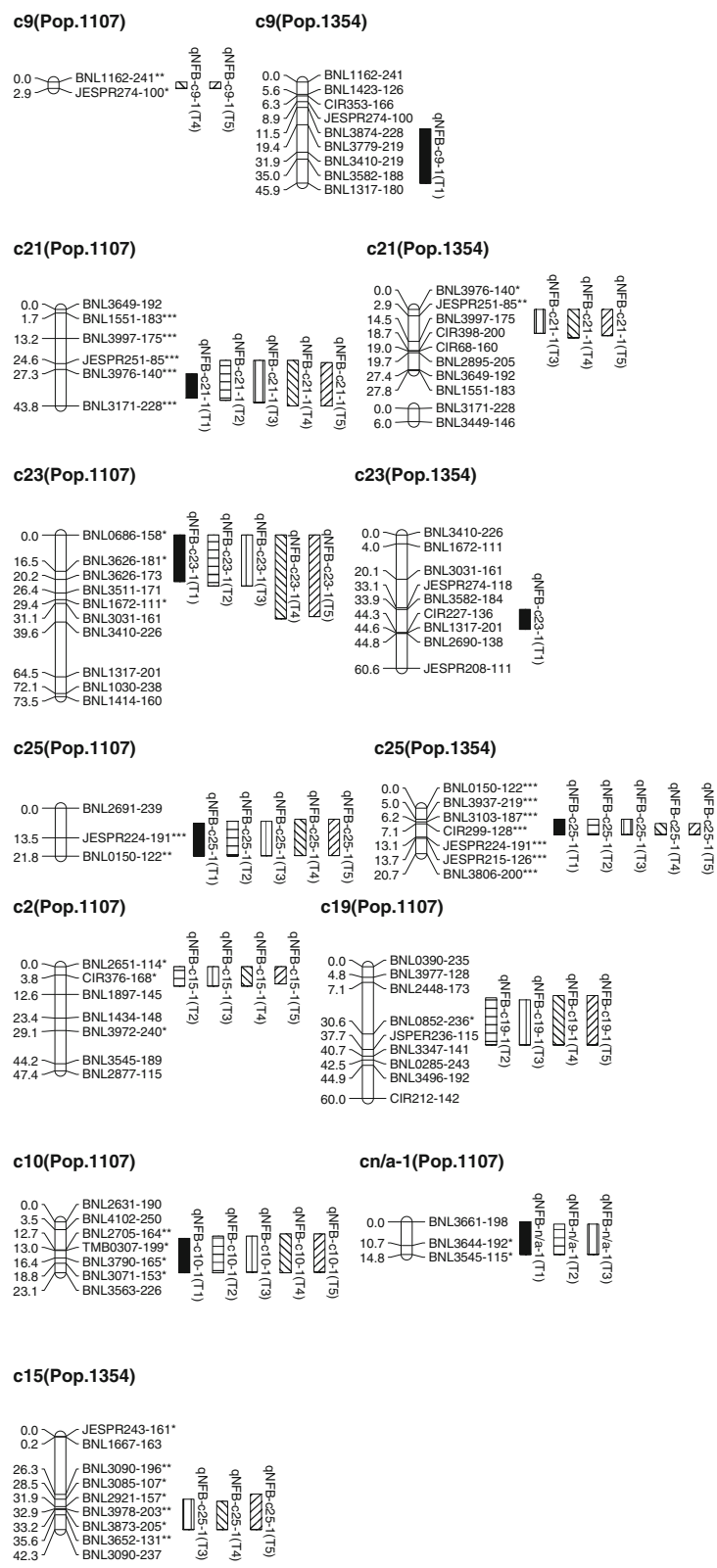

Fig. 1 Distribution of QTLs at the five scoring dates in the two populations that were detected by interval mapping. T1, T2, T3, T4, and T5 represent 73, 84, 101, 112, and 129 DAP, respectively. *, **, and *** denote K–W test for marker and trait association at 0.05, 0.01, and 0.001 probability level, respectively. The cn/a is a linkage group not assigned to a specific chromosome

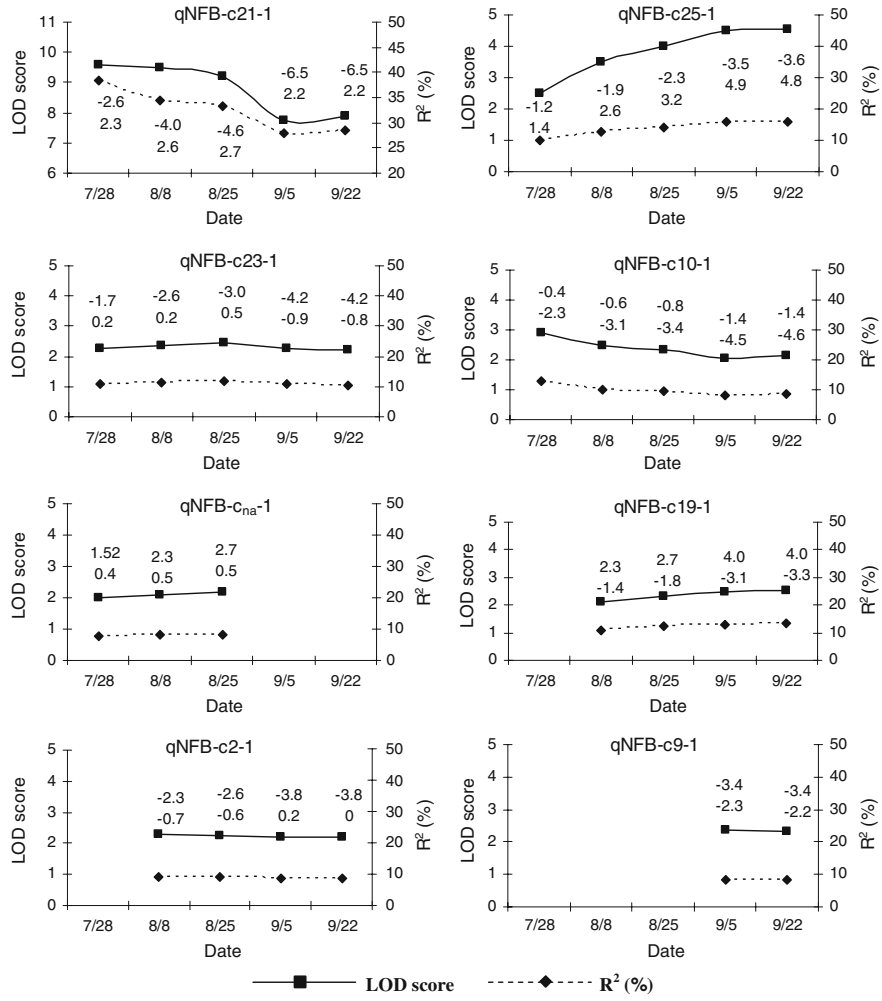

Fig. 2 LOD score and R^2 of QTLs for NFB in Pop. 1107. The upper and lower numbers at each time point present the additive and dominance effects, respectively. Positive value indicate allele from DPL61 increase NFB, negative value indicate that allele from T1107 increase NFB

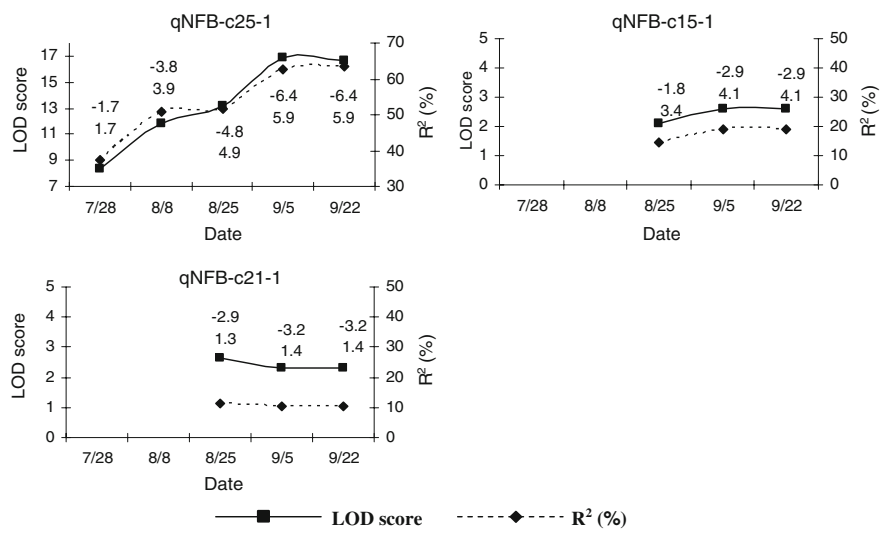

Fig. 3 LOD score and R^2 of QTLs for NFB in Pop. 1354. The upper and lower numbers at each time point present the additive and dominance effects, respectively. Positive value indicate allele from DPL61 increase NFB, negative value indicate that allele from T1354 increase NFB

indicated they were probably common in both populations (Fig. 1). Comparing the results of both populations with our previously study on another Upland cotton accession, T701 (Guo et al. 2008a), some QTLs were defined by same markers interval or by closely linked markers. It might suggest that they were located in a common region, especially the QTL on chromosome 25. However, conservation of QTL position could not guarantee that genes responsible for the QTLs were the same.

Deriving mapping populations suitable for replication phenotyping was impeded by the difficulty of flowering and followed seed production under normal day length condition. However, repeated observations on the same individual during different time and comparing different mapping populations derived from the common female parental line were forms of replication, and consequently increased the confidence of detected QTLs (Bradshaw and Foster 1992; Verhaegen et al. 1997; Wu et al. 1999).

Genetic effects from single marker regression analyses are shown in Tables 3 and 4. In Pop. 1107, markers on chromosome 21 and 25 individually accounted for more than 10% of the phenotypic variation for NFB (Table 3). Stepwise regression analyses showed that two markers on chromosome 21 (BNL3976-140 and BNL3171-228) and one marker on 25 (JESPR224-191) together accounted for 42.4% of the phenotypic variation. Further adding another four markers (seven in total) on chromosome 2 (CIR376-168), 9 (BNL1162-241), 19 (BNL0852-236), and 23 (BNL1672-111), they accounted for 54.9% of the phenotypic variation for NFB. In Pop. 1354, only markers on chromosomes 2, 15, 21, and 25 individually accounted for more than 10% of the phenotypic variation for NFB (Table 4). Using stepwise multiple regression analysis, two markers (CIR299-128 and JESPR224-191) on chromosome 25 together accounted for 61.3% of phenotypic variation. Including the two markers on chromosome 25 and

Table 3 Genetic effects and coefficients of determination associated with single markers and QTLs at 129 DAP for Pop. 1107 by regression analysis

Marker	Chromosome	R^2	Additive effect[a]	Dominance effect
BNL2651-114	2	0.055**	−2.38**	–
CIR376-168	2	0.067*	−3.49**	−1.30
BNL3972-240	2	0.055*	−1.20	3.52*
BNL2705-164	10	0.075**	−2.21*	−3.40*
TMB0307-199	10	0.069*	−2.08	−3.32*
BNL3790-165	10	0.053*	−1.39	−3.50*
BNL3071-153	10	0.061*	−1.18	−3.74*
BNL2449-141	18	0.065*	0.67	4.49**
BNL0852-236	19	0.066*	2.85**	−1.64
BNL1551-183	21	0.109***	−3.42***	2.81
BNL3997-175	21	0.133***	−4.27***	2.50
JSPER251-85	21	0.225***	−5.51***	3.52*
BNL3976-140	21	0.224***	−5.22***	3.83**
BNL3171-228	21	0.233***	−6.16***	1.92
BNL0686-158	23	0.071*	−3.50**	0.48
BNL3626-181	23	0.059**	2.37**	–
BNL1672-111	23	0.070*	−3.31**	−1.45
BNL3031-161	23	0.058*	−2.53*	−2.26
BNL1162-241	9	0.096**	−3.63**	−2.52
JESPR274-100	9	0.083**	−3.46**	−1.95
BNL2691-239	25	0.072*	−2.62*	2.79
JESPR224-191	25	0.171***	−3.73***	5.00**
BNL0150-122	25	0.120***	−4.29***	2.30
BNL3644-192	Unknown	0.052*	3.07*	0.43
BNL3545-115	Unknown	0.061*	3.45**	0.04

*,**,*** Denotes significance at ≤0.05, ≤0.01, and ≤0.001 level, respectively

[a] Positive additive value indicate that allele from DPL61, a day-neutral commercial cultivar, increase NFB, negative value indicate that allele from T1107 increase NFB

Table 4 Genetic effects and coefficients of determination associated with single markers and QTLs at 129 DAP for Pop. 1354 by regression analysis

Marker	Chromosome	R^2	Additive effect[a]	Dominance effect
BNL1434-246	2	0.106*	−5.20**	4.45*
BNL1552-160	5	0.095*	−4.75**	2.33
BNL0625-237	11	0.091*	−5.95	10.29**
BNL0226-225	14	0.061*	−8.25*	5.93
BNL3090-196	15	0.087**	−2.27**	–
BNL3085-107	15	0.091*	3.93	0.53
BNL2921-157	15	0.092*	−2.20*	2.49
BNL3978-203	15	0.096**	−2.72*	1.66
BNL3873-205	15	0.094**	−2.64*	1.81
BNL3652-131	15	0.124**	4.10	1.23
BNL4082-169	15	0.082*	−4.11*	2.93
BNL1721-188	18	0.084*	−2.49	6.04*
BNL3347-141	19	0.075*	1. 80	−2.67
BNL3171-228	21	0.096*	2.05	4.32
BNL3449-146	21	0.117**	4.06	3.28
BNL3410-219	9	0.055*	−2.02*	–
BNL0597-192	9 or 23	0.087*	−8.54*	4.92
BNL2884-162	24	0.077*	−2.57*	−1.62
BNL0150-122	25	0.432***	6.15*	5.89*
BNL3937-219	25	0.532***	−6.11***	4.18***
BNL3103-187	25	0.500***	−5.89***	3.97***
CIR299-128	25	0.523***	2.74**	9.66***
JESPR224-191	25	0.433***	3.96***	8.02***
JESPR215-126	25	0.131***	−1.93	−4.07**
BNL3806-200	25	0.254***	3.50**	5.04**
BNL0598-124	12 or 26	0.090*	−4.84**	6.47**
BNL3445-71	Unknown	0.070*	−7.00*	9.18*

*,**,*** Denotes significance at ≤0.05, ≤0.01, and ≤0.001 level, respectively

[a] Positive additive value indicate that allele from DPL61, a day-neutral commercial cultivar, increase NFB, negative value indicate that allele from T1354 increase NFB

two additional makers BNL3090-196 (chromosome 15) and BNL3449-146 (chromosome 21), the total R^2 value increased to 68.5%. No significant epistatic QTLs and loci interactions were detected in either population. However, epistasis was detected between markers on chromosome 16 and 21 or markers on chromosome 16 and 25 in our previous study (Guo et al. 2008a). This may indicated the different gene interaction patterns existed in different accessions.

Although the genetic architecture of NFB in cotton is only partially known, it more likely involves the action of several genes. A fundamental question for complex adaptive traits is whether each gene has a uniform and small effect or whether there are a small number of genes explaining a large proportion of the variation. In this study, in view of the fact that each population had one or two major QTLs explaining from 15.9 to 63.5% of the phenotypic variation for NFB, the second hypothesis is likely. Moreover, many of the adaptive traits of other plants also suggested a few major QTLs explained a large proportion of the phenotypic variation (Doebley and Stec 1991; Koinange et al. 1996; Kuittinen et al. 1997; Voss and Shaffer 1997; Poncet et al. 2000; Peng et al. 2003). Although the adaptive traits mechanism remained unclear, it could be that during plant evolution, when species invaded new niches, large effects could be common (Orr 1998; Doebley et al. 2006). But this conclusion should be regarded with caution (Paterson 2002). For photoperiodic accessions in which the trait (low NFB) was mainly controlled by a small number of QTLs, it should be relatively straightforward to introgress early day-neutral genes into these germplasm. However, linkage drag has been detected because of the possible complex genetic nature of flowering time. Liu et al. (2000) investigated 97 day-neutral derived

race stocks, and found the majority of the accessions shared more than 75% of the same SSR marker alleles as TM-1 (a genetic standard of Upland cotton) even after four backcrosses. Zhong et al. (2002) also found that day-neutral derivatives of photoperiodic accessions carried more alleles from the day-neutral parent than from the accession parents. Future studies on linkage drag will help a better understanding of the mechanism of cotton photoperiodic sensitivity.

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